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Habitat selection can reduce effects of extreme climatic events in a long-lived shorebird

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Abstract:

1. Changes in the frequency of extreme climatic events (ECEs) can have profound impacts on individual fitness by degrading habitat quality. Organisms may respond to such changes through habitat selection, favouring those areas less affected by ECEs; however, documenting habitat selection in response to ECEs is difficult in the wild due to the rarity of such events and the long-term biological data required.
2. Sea level rise and changing weather patterns over the past decades has led to an increase in the frequency of coastal flooding events, with serious consequences for ground nesting shorebirds. Shorebirds therefore present a useful natural study system to understand habitat selection as a response to ECEs. We used a 32-year study of the Eurasian oystercatcher (*Haematopus ostralegus*) to investigate whether habitat selection can lead to an increase in nest elevation and minimise the impacts of coastal flooding.
3. The mean nest elevation of *H. ostralegus* has increased during the last three decades. We hypothesised that this change has been driven by changes in *H. ostralegus* territory

settlement patterns over time. We compared various possible habitat selection cues to understand what information *H. ostralegus* might use to inform territory settlement.

4. There was a clear relationship between elevation and territory settlement in *H. ostralegus*. In early years, settlements were more likely at low elevations but in more recent years the likelihood of settlement was similar between high and low elevation areas. Territory settlement was associated with conspecific fledgling output and conspecific density. Settlement was more likely in areas of high density and areas with high fledgling output.
5. This study shows that habitat selection can minimise the effects of increasingly frequent ECEs. However, it seems unlikely that the changes we observe will fully alleviate the consequences of anthropogenic climate change. Rates of nest elevation increase were insufficient to track current increases in maximum high tide (0.5 v. 0.8 cm/year). Furthermore, habitat selection cues that rely on information from previous breeding seasons (e.g. conspecific fledgling output) may become ineffective as ECEs become more frequent and environmental predictability is diminished.

Key words: Flood; extreme events; habitat selection; salt marsh; climate change; *Haematopus ostralegus*; waders

Introduction:

Anthropogenic climate change has the potential to dramatically alter patterns of habitat quality. Rapid changes in climatic conditions can lead to the degradation of previously suitable habitats (Davies, Wilson, Coles, & Thomas, 2006; Pike & Stiner, 2007), which can have consequences for organismal reproductive success, survival, and overall fitness (Wilson, 1998; Silberbush & Blaustein, 2011). One factor that may lead to declines in habitat quality will be the increased frequency of

extreme climatic events (ECEs) (Coumou & Rahmstorf, 2012), with such events having major impacts on survival and reproduction (Parmesan, Root, & Willig, 2000). However, while the potential threat of ECEs is well understood (Bailey & van de Pol, 2016; Coumou & Rahmstorf, 2012; Parmesan et al., 2000), it is less clear whether organisms have the capacity to respond as ECEs become more frequent. Understanding if and how organisms can respond to more frequent ECEs will be critical to identify those species and populations most at risk from anthropogenic climate change.

Box 1: Definitions of key terms used in the manuscript.

Term	Definition
Habitat selection	The active choice of habitat by an organism based on cues that inform individuals of the fitness costs and benefits associated with a given habitat.
Habitat selection strategy	The set of environmental cues (abiotic and biotic) used by an organism to inform habitat selection.
Territory settlement	In *Haematopus ostralegus,* the behavioural process by which a pre-breeding adult first enters the breeding population and establishes a territory.

Behavioural responses may allow species to mitigate some of the potential effects of increasingly frequent ECEs, either during the event itself or after the event has passed (Wingfield et al., 2017). ***Habitat selection*** (Box 1), the active choice of habitat by an organism, is one behavioural mechanism that can mitigate the effects of ECEs. For example, birds living in arid habitats can minimise the acute effects of extreme heat events by changing micro-habitat use (R. O. Martin, Cunningham, & Hockey, 2015). Organisms may also minimise future ECE impacts by selecting those habitats less vulnerable to ECEs, in a similar way to which organisms can respond to other stochastic events such as predation (Thomson, Forsman, Sardà-Palomera, & Mönkkönen, 2006). To use habitat selection as a mechanism for minimising ECE impacts, organisms require a reliable ***habitat selection strategy*** (Box

1), a set of environmental cues that can inform them of the fitness costs and benefits associated with a given habitat. However, if environmental conditions change substantially, organisms may end up ecologically 'trapped' using unreliable habitat selection strategies that are now maladaptive (Robertson & Hutto, 2006). Such maladaptive strategies may occur if organisms are incapable of assessing the vulnerability of habitats to ECEs or because organisms simply underestimate the increased risk of ECEs under anthropogenic climate change and thus fail to respond. Currently, it is not clear whether habitat selection strategies that can effectively mitigate the detrimental effects of ECEs are common in wild organisms.

Changes in habitat selection as a response to increasing ECE frequency may occur through both inter-generational micro-evolutionary change (i.e. the evolution of new habitat selection strategies) and phenotypic plasticity (i.e. the use of existing habitat selection strategies) (Schlaepfer, Runge, & Sherman, 2002). The effectiveness of these different mechanisms will depend greatly on the species in question. For example, rapid habitat degradation will limit the effectiveness of micro-evolutionary responses, particularly in species with long generation times, as rates of micro-evolutionary change will be too slow to track rapid changes in habitat quality (Kokko & Sutherland, 2001). Habitat selection strategies that include learning may present a more rapid mechanism through which organisms can respond to increasing ECE frequency. An individual may learn from both their own experiences and also from observing other individuals (Danchin, Giraldeau, Valone, & Wagner, 2004; Valone, 2007). Using information available from conspecifics is considered a particularly effective mechanism through which individuals can track environmental change (Kokko & Sutherland, 2001; Ponchon, Garnier, Grémillet, & Boulinier, 2015), because it integrates a broad range of biotic and abiotic factors (Pärt & Doligez, 2003; Valone, 2007) and removes the need for individuals to have direct experience in all habitats (Danchin et al., 2004; Valone, 2007).

In this paper, we study changes in habitat selection using a 32-year individual-based dataset of a long-lived shorebird, the Eurasian oystercatcher (*Haematopus ostralegus*). Over the course of the study, sea level rise and changing wind and storm patterns have led to a rapid increase in the frequency of extreme flooding events, from once every 7.0 years, between 1971 and 1991, to once every 2.7 years since 1991, equivalent to an increase in the maximum high tide of 0.8 cm/year (van de Pol et al., 2010; Bailey et al., 2017). Extreme flooding events have severe consequences for breeding pairs, washing away eggs and drowning young chicks (van de Pol et al., 2010). Future increases in flooding frequency are predicted to decrease the viability of the study population (van de Pol et al., 2010). However, *H. ostralegus* breeding pairs can reduce the effects of extreme flooding events by nesting at higher elevations (van de Pol et al., 2010).

In our previous work, we predicted that individual *H. ostralegus* pairs would show an increase in nest elevation over their lifetime, selecting higher elevation nesting sites to minimise the consequences of more frequent flooding events. However, contrary to our prediction, we found that breeding adults have shown little change in nest elevation over their lifetime (Bailey et al., 2017). Despite these results, mean nest elevation of the population has still increased over the study period (see Results), which suggests that other mechanisms may be driving nest elevation change. Our previous work excludes the possibility that the observed patterns are a consequence of changes in nesting sites or territory movement during an individual's lifetime. Instead, we hypothesise that habitat selection of new birds entering the population for the first time may provide an alternative explanation.

When *H. ostralegus* individuals first enter the breeding population they select an area in which to establish their breeding territory. Once established, territory movement is infrequent (Heg, Ens, van Der Jeugd, & Bruinzeel, 2000; Bruinzeel, 2007). On average, territory locations move only around 60m during an individual's lifetime, which is small compared to the overall territory size (median territory size: 2,551m^2; see Methods for more details). Cases of intermittent breeding, where an

individual is forced to leave the breeding population and re-settle in a later year, are infrequent (~4% annually), and re-settlement tends to occur very close to original territory (Bruinzeel, 2007). Expansion of established territories is also difficult because neighbouring pairs aggressively defend their territory boundaries (Ens, van de Pol, & Goss-Custard, 2014). This means that breeding pairs are constrained to use nesting sites within their established territory and ***territory settlement*** (Box 1) of new birds will have a strong effect on future nesting conditions, including nest elevation. If birds entering the population begin to settle more often in high elevation areas, this will increase the proportion of high elevation nests and, subsequently, the mean nest elevation of the population. In this way, changes in territory settlement could explain the observed increases in nest elevation.

The mean nest elevation of the population could also change through selective territory vacancy. If low elevation territories are vacated more often than those at high elevation (and are not filled by new recruits) then the proportion of high elevation nests and the mean nest elevation of the population will increase. Territory vacancy occurs when breeders disappear from the population, due to either death or dispersal. Territory vacancy and settlement are inter-related because vacated territories create opportunities for new birds to settle. However, patterns of vacancy and settlement differ in some ways. Vacated territories may be engulfed by those of their neighbours rather than being settled by new birds. Similarly, new territory settlements can occur when *H. ostralegus* pairs take over a section of an already occupied territory (Heg et al., 2000). Therefore, it is important to distinguish between territory settlement and vacancy to understand the mechanisms behind *H. ostralegus* nest elevation change.

To investigate how territory settlement may affect nest elevation, we first quantified the rate of nest elevation change within our population during the past three decades. Next, we tested whether territory settlement and/or vacancy are related to elevation and whether this relationship has changed over time. We predicted that territory settlement would be strongly affected by elevation, because low elevation territories will be at a greater risk of flooding and so will provide poor quality

breeding sites. In comparison, we predicted that territory vacancy would be unaffected by elevation as we expected vacancies to mostly be a consequence of adult mortality, which should be independent of territory elevation.

Finally, we compared the role of elevation in territory settlement to other potential cues. We considered four different cues that individuals might use to inform territory settlement. First, *H. ostralegus* may directly evaluate flooding risk when selecting a territory. We predicted that individuals should show a greater preference for high elevation sites over time. Second, individuals may consider proximity to food resources during territory settlement. Breeding territories near to the coastline or tidal gullies have direct access to food resources allowing breeding pairs to easily provision their offspring. We predicted that individuals should favour territories close to these two food resources. It is worth noting that coastal proximity and elevation are not synonymous, with many low elevation sites found inland (see Methods; Fig. S1). Third, individuals may base their territory settlement decisions on the reproductive output of existing conspecific breeding pairs (hereafter 'conspecific fledgling output'). If conditions in one breeding season are predictive of the next breeding seasons, we would expect individuals to settle more often in areas that produced a relatively high number of fledglings. This may also allow individuals to minimise flooding risk because flooded areas will have a low fledgling output. Finally, individuals may use conspecific density as a cue to inform territory settlement, which may allow some assessment of habitat quality without requiring direct observation of fledglings. We predicted that settlements would be more likely in more densely populated areas. These four cues are not mutually exclusive, and all may be utilised by *H. ostralegus*.

Methods:

Study system

H. ostralegus is a widespread ground nesting Eurasian shorebird that regularly breeds on salt marshes and beaches, close to the intertidal mudflats on which it feeds. It is a long-lived species (generation time 13 years), and forms stable, long-term pair bonds (van de Pol, Heg, Bruinzeel, Kuijper, & others, 2006). Breeding pairs establish exclusive territories that they occupy during the breeding season (i.e. a territory cannot include multiple breeding pairs). Breeding pairs show strong territory fidelity, generally returning to the same breeding territory each year, and aggressively defend their territory boundaries from conspecifics (Ens et al., 2014; van de Pol, Bruinzeel, Heg, Van Der Jeugd, & Verhulst, 2006). *H. ostralegus* breeding pairs lay eggs in shallow nest scrapes located within their territory boundaries (del Hoyo, Elliott, & Sargatal, 1992). New nests are built each year and nest locations often move, but locations are restricted to within a pair's territory. As *H. ostralegus* does not construct nest mounds and uses limited nesting material, nest elevation is the elevation of the location used for nesting. Available territories are limited, and those individuals that fail to establish a territory are unable to breed (Heg et al., 2000; van de Pol, Pen, Heg, & Weissing, 2007).

Territory quality varies widely, due to both flooding risk (van de Pol et al., 2010) and distance to intertidal feeding sites (Ens, Kersten, Brenninkmeijer, & Hulscher, 1992; Schwemmer, Weiel, & Garthe, 2017). Breeding pairs with territories adjacent to the intertidal mudflats can directly provision their offspring, while inland pairs must collect food from the intertidal mudflats and bring them back to their offspring in the nesting territory (Ens et al., 1992). The cost of provisioning for inland territories increases with distance from the shoreline due to travel time associated with each foraging trip (Schwemmer et al., 2017), and so coastal territories can produce around three times more fledglings than inland territories (Ens et al., 1992; van de Pol, Bruinzeel, et al., 2006). It is important to note that distance to the mudflats is not a direct indicator of flooding risk. Median

territory elevation and coastal distance are not strongly correlated (r = 0.51), and nest elevation of birds with coastal and inland territories show considerable overlap (Fig. S1). Therefore, selecting higher elevation territories will not necessarily equate to moving further from the mudflats.

This study was conducted on a population of *H. ostralegus* breeding on the Dutch barrier island of Schiermonnikoog in the Wadden Sea (53.4833° N, 6.1667° E). Over 90% of *H. ostralegus* individuals breeding within the study area have been individually colour banded, allowing their behaviour to be followed over multiple years. The population has been monitored consistently since 1983, during which time numbers have declined both within our study population and across the region, with declines of 3% per annum across the Wadden Sea region between 1991 and 2009 (van de Pol, Atkinson, Blew, & others, 2014; van Roomen et al., 2012). Because of these declines, the study area has been expanded over time to sample a similar number of breeding pairs each year. We divided the study site into nine separate sub-areas that have been monitored for different lengths of time. These different sub-areas varied in their elevation and location (i.e. proximity to the coastline), which was accounted for in our analyses (see below). Although population numbers have declined, the size of territories has expanded (Fig. S2), and the study area should be considered fully occupied in all years.

Data collection

We monitored nesting activity of *H. ostralegus* annually from April to August. Nests were located through systematic searching every 2 – 3 days, and parents were identified by their colour bands. From 1984, the identity of all breeding pairs and the approximate location of their breeding territories were recorded on a detailed coastal map. Since 1986 all nests were also plotted on the coastal map and from 2000, nest coordinates were recorded precisely using GPS. We measured the elevation of *H. ostralegus* nests over a 22-year period (1995 – 2016; no data in 1997 - 1999) in centimetres above a reference point, here chosen as mean high tide in 1971 (hereafter MHT; the first year in which water height data are available; source www.live.waterbase.nl). We collected nest

elevation data from 3,221 nests of which 2,544 had at least one banded parent. In total, we had nest elevation data from 403 banded males and 434 banded females.

The methods used to measure nest elevation varied between years. In ten years (1995, 1996, 2008, & 2010-2016) we measured nest elevation directly in the field. Elevation was determined in-situ using a water level device (1995 – 1996); laser machine control device (2008); and a differential GPS (2010 – 2016; ProMark 800 GNSS). All in-situ methods provide measurement accuracy to within 2cm, confirmed using existing calibration sites established by the Dutch Ministry for Infrastructure and Environment (Rijkswaterstaat). For all other nests, we determined elevation by overlaying GPS coordinates of nests on a LiDAR digital elevation map (measured 2008; cell size 0.5 m x 0.5 m; http://www.ahn.nl/index.html). This ex-situ method was used to collect data between 2000 – 2007 and 2009, as well as supplementing data in predominantly in-situ measured years. We expected that both the precision and accuracy of our ex-situ method would be lower than our in-situ methods and this was accounted for in our statistical models (see below).

To determine the elevation characteristics of nesting territories, we constructed territory polygons using information on the known location of individual pairs in each year (nest coordinates in combination with georeferenced territory and nest maps). Polygons were generated using a Voronoi equation (Aurenhammer, 1991), which is known to provide a reasonable estimate of territory characteristics in birds (Grabowska-Zhang, Sheldon, & Hinde, 2012; Schlicht, Valcu, & Kempenaers, 2014). The median area of territory polygons was 2,551m^2 (range 1 – 97,760m^2), with territory area increasing by an order of magnitude over the study period (Fig. S2 – S3). Territory polygons were overlayed on the LiDAR digital elevation map, from which we calculated median territory elevation (cm above MHT; n = 3,423 territories). As we have no record of *H. ostralegus* nests less than 20 cm above MHT, all points below 20 cm were considered unviable nesting locations and were excluded from our calculations.

For all our analyses we considered the behaviour of males rather than females, as male identity has been shown to have a stronger influence on nest elevation than female identity (Bailey et al., 2017). In previous analyses of *H. ostralegus* nest elevation, results were qualitatively similar between males and females (Bailey et al., 2017), so we consider our results to be representative of both sexes. To study territory settlement of males, we divided our study site into a grid of 50m x 50m squares (0.25 ha/2,500 m^2), which corresponds to the median territory area observed in the population. For each grid square, we determined the median elevation (using the LiDAR map), distance to the coast, and distance to the nearest gully (an alternative food source). When a new male was seen to settle in the breeding population, we determined the centre point of the newly settled territory and identified the corresponding grid square. Territory settlement is an individual's first settlement in the breeding population (Box 1), excluding infrequent cases of intermittent breeding where an individual is forced to leave the breeding population, due to divorce or widowing, and re-settle in a later year (~4% annually) (Bruinzeel, 2007). In total we obtained data on territory settlement in 9,376 grid squares across our 32-year study period, with 259 settlements observed over this time. In each year we determined whether at least one settlement had occurred in each grid square and this binary variable was used as the response in our statistical models (see below).

To study territory vacancy by males, we identified all cases where a banded breeding male disappeared from the population and was not re-observed during the remainder of the study period. Resighting probability of breeding birds is greater than 99% (van de Pol, Bruinzeel, et al., 2006; van de Pol et al., 2010), so we can have high confidence that an unsighted bird is not present in our study area and is either dead or has dispersed to another breeding population. Incidences of adult dispersal outside of the study area occur almost exclusively during the pre-breeding period (i.e. before territory settlement), so it is likely that most territory vacancies will be caused by adult mortality rather than dispersal (van de Pol, Bruinzeel, et al., 2006). Our territory vacancy data included 3,056 territory-year combinations from 465 banded males. Over the 32-year period of our study we observed 357 territory vacancies.

We calculated conspecific density and conspecific fledgling output as potential cues informing settlement decisions. Annual territory density was calculated as the number of territory centre points within each grid square. This value was mean centred within each year to provide a relative measure of annual territory density. The number of fledglings produced by each breeding pair was recorded during regular nest checks. In cases where breeding pairs were observed but no nest was found we assigned the breeding pair to have the most common number of fledglings from all monitored pairs in the same year. These cases constituted 19% of all territory records. We calculated the annual average number of fledglings produced per breeding pair within each grid square, which was mean centred within each year to determine relative annual fledgling output.

To quantify patterns of territory movement (discussed in the Introduction) we extracted the centre point of all territory polygons associated with a banded male. We then determined the maximum distance that territory centre points moved during the lifetime of every male. On average, territories moved a maximum of 60.6m during an individual's lifetime (range 2.1 – 1169.1m; Fig. S4).

Change in nest elevation over time

To quantify change in mean nest elevation over time, we used a general linear mixed effects model with a Gaussian distribution in the R package *spaMM* (Rousset & Ferdy, 2014). We included random intercepts for male identity and study sub-area (9 sub-areas) and tested the change in nest elevation over time using a continuous year variable. We allowed for heteroscedasticity as a function of measurement method to account for differences in precision between in-situ and ex-situ measurements (see above). We also included measurement method as a fixed term in our model to account for systematic measurement bias that may occur between our two methods. Nest elevation (cm above MHT) was transformed with a Box-Cox transformation (λ = -0.45) to produce normality in model residuals.

Relationship between elevation and territory settlement and vacancy

To investigate the relationship between territory settlement and elevation we fitted a generalised linear mixed effects model with a binomial distribution (logit link) in the R package *spaMM* (Rousset & Ferdy, 2014). Our model included a logarithmic effect of median elevation and a continuous year term. We included a logarithmic term as we expected the impact of elevation on territory quality to diminish exponentially once nests are above average flooding heights. We also included an interaction between year and elevation to test whether the relationship between settlement and elevation has changed over time. The model included a term that accounted for differences in suitable habitat between grid squares (i.e. total area within each grid square greater than 20 cm above MHT). We also included a random intercepts term for the nine study sub-areas in our model to account for differences in which sub-areas were monitored in different years. To ensure results were robust to grid size we also ran our analyses using a coarser 100 m x 100 m (1 ha) grid.

Analysis of territory vacancy was conducted with a similar generalised linear mixed effects model with a binomial distribution (logit link). In addition to the variables included in the model of territory settlement, analysis of territory vacancy also included a further term for territory quality (coastal or inland). Inland territories are generally poorer quality than coastal territories (see above), which may affect territory vacancy rates.

Comparing settlement cues

To investigate the cues that drive territory settlement we conducted model selection using conditional AIC values (CAIC) that are designed for use with mixed-effects models (Vaida & Blanchard, 2005). All models had the same basic structure as described above. We included variables to test for four potential cues: 1) direct flooding risk (logarithmic elevation plus an elevation x year interaction term, as seen above), 2) food availability (logarithmic effect of coastal distance and gully distance); 3) conspecific fledgling output; and 4) conspecific density. We included a logarithmic

effect of coastal and gully distance as we expected the impact of these variables on territory quality to diminish exponentially once breeding pairs are no longer able to access food resources. As *H. ostralegus* make habitat selection decisions before breeding begins, we assumed that individuals would use conspecific density and conspecific fledgling output information from the preceding years to inform settlement decisions. Prospecting pre-breeders may assess territory quality over multiple years before recruiting into the breeding population (Ens, Weissing, & Drent, 1995; van de Pol, Bruinzeel, et al., 2006); therefore we considered the mean density and fledgling output in each grid square over the past 3 years. This necessarily required us to reduce the amount of data in our analysis, as we could only consider settlement in areas that had been surveyed over the past three years. Therefore, for the analysis of settlement cues, we used a subset of the data that included 167 settlement events between 1987 and 2016.

Multicollinearity and confidence intervals

We determined variance inflation factors for variables in all models to avoid issues of multi-collinearity. We considered variables to have issues of multi-collinearity when variance inflation factors were above 3. Multi-collinearity was not an issue in any of the fitted models.

We calculated 99.5% confidence intervals, following suggestions of Benjamin et al. (Benjamin et al., 2018), in addition to less conservative 95% confidence intervals.

For a mathematical representation of models used see Appendix 1.

Software

All analyses were conducted using R v3.5.2 (R Core Team, 2017) in RStudio (v. 1.0.153). All R packages that were used but not mentioned above are listed here with appropriate attribution:

dplyr (Wickham, Francois, Henry, & Muller, 2017), DHARMa (Hartig, 2017), extrafont (Chang, 2014), plotly (Sievart et al., 2017), raster (Hijmans, 2016), rgdal (Bivand, Keitt, & Rowlingson, 2017), rgeos (Bivand & Rundel, 2017), ggplot2 (Wickham, 2016).

Results:

Change in nest elevation over time

H. ostralegus nest elevation increased over time (Fig. 1; Table S1). After accounting for Box-Cox transformation (λ = -0.45) nest elevation changed at a mean rate of 0.52cm/year (range: 0.46 – 0.58 cm/year).

Relationship between elevation and territory settlement and vacancy

The relationship between elevation and probability of *H. ostralegus* territory settlement changed over time (Fig. 2; Table S2). In early years, settlements were more likely at lower elevations; however, in later years the probability of settlements was no longer affected by elevation. Results were qualitatively similar when using 1 ha grid squares (Table S2).

On average, 11% of males vacated territories each year (Fig. S6), which is similar to annual mortality rates previously estimated for this population (Camphuysen et al., 1996; van de Pol, Bruinzeel, et al., 2006; Zwarts, Hulscher, & Koopman, 1997). Male vacancy tended to be positively related to elevation in early years (i.e. higher elevation territories were more likely to be vacated), but this changed in later years, so that male vacancy was more often observed at low elevation sites (Fig. 3). However, the interaction effect was not supported using either of our two measures of confidence and measures of model fit (marginal and conditional R^2) were low (Table S4). Therefore, it seems unlikely that patterns of territory vacancy have been driving the observed increase in nest elevation. Inland territories were more likely to be vacated than coastal territories (Table S4).

Comparing settlement cues

Conspecific density and conspecific fledgling output were included in all top models in our model selection procedure (ΔCAIC < 2; Table 1). Probability of *H. ostralegus* settlement increased with higher conspecific density and fledgling output (Fig. 4; Table S5). Effects were qualitatively similar when using larger grid squares (Table S5). Models including elevation and coastal/gully distance were indistinguishable from those models with these terms removed (< 2 CAIC), suggesting that these cues were less important determinants of territory settlement. The top model from our model selection table was qualitatively similar when using 1 ha grid squares (Table S5). An illustration showing spatial patterns of territory settlement in relation to elevation, conspecific density and conspecific fledgling output can be seen in Fig. S7.

Discussion:

We found that *H. ostralegus* territory settlement has changed over the past three decades. In early years, new settlements were much more likely in low elevation areas (Fig. 2). Around the turn of the century, however, settlement probability was similar between the highest and lowest areas. This helps explain the increase in mean nest elevation observed over the study period (Fig. 1) and suggests that habitat selection can provide a mechanism through which species can respond to extreme climatic events (ECEs). However, elevation itself does not appear to be the most prominent habitat selection cue in this species, with conspecific density and fledgling output having a stronger influence on settlement patterns (Fig. 4). Therefore, it appears that observed changes in territory settlement are not an example of direct avoidance of ECEs but rather a response to the consequence of flooding events, such as reduced fledgling output. Despite the encouraging changes seen in our population, it is unclear whether this habitat selection strategy will provide a long-term mechanism by which *H. ostralegus* can avoid ECEs.

Relationship between elevation and territory settlement and vacancy

Our results suggest that species may be able to respond to changing patterns of ECEs without the need to develop completely novel habitat selection strategies. The evolution of novel habitat selection strategies would require multiple generations, which may be insufficiently slow as a response to rapid anthropogenic climate change, particularly in long-lived species like *H. ostralegus* (Kokko & Sutherland, 2001).

Unlike habitat selection, territory vacancy did not show any relationship with elevation. We can be confident, therefore, that the observed increase in nest elevation over the past decades is driven by habitat selection rather than adult death or dispersal. The lack of a clear elevation pattern in territory vacancy is in agreement with our expectations as we assumed most territory vacancies would be caused by adult mortality. Flooding events can lead to the loss of eggs and chicks (van de Pol et al., 2010) but pose no threat to adult birds and so mortality rates should be independent of elevation and flooding risk. The rates of territory vacancy we observed here (11%) were similar to mortality rates estimated previously in this population (Camphuysen et al., 1996; van de Pol, Bruinzeel, et al., 2006; Zwarts et al., 1997), further supporting our expectation.

Comparing settlement cues

Conspecific density and fledgling output appear to be the major cues used by *H. ostralegus* during territory settlement. Using information from the experiences of conspecifics is hypothesised to be a common habitat selection strategy, as it allows for habitat selection decisions without the need for an individual to have direct experience in a given habitat (Danchin et al., 2004; Kokko & Sutherland, 2001; Pärt & Doligez, 2003; Ponchon et al., 2015; Valone, 2007). Making habitat selection decisions without direct reproductive experience will be necessary for pre-breeding *H. ostralegus* individuals as they have no prior breeding experience to draw from. Fledgling output will allow individuals to

assess conditions in the recent breeding seasons preceding settlement. In comparison, conspecific density will allow pre-breeders to assess territory quality over a longer time-scale as it reflects the settlement decisions made by many other pre-breeders in previous years. In combination, these cues will allow *H. ostralegus* individuals to assess a range of biotic and abiotic factors that influence reproductive success, including flooding risk (Pärt & Doligez, 2003; Valone, 2007).

We found less evidence that pre-breeding birds use elevation as a cue during habitat selection. Therefore, it seems that increases in nest elevation observed in *H. ostralegus* may not be a direct response to ECE vulnerability, but rather a response to the nest failure and low fledgling output that are a consequence of increased flooding. Although elevation appears to play little role in *H. ostralegus* habitat selection, it is possible that individuals may still be able to assess direct flooding risk using other cues. For example, vegetation type and height can act as cues for flooding risk as they are directly influenced by flooding patterns (Pennings, Grant, & Bertness, 2005). Vegetation characteristics will also provide information on predation risk as they will affect nest concealment and camouflage (Troscianko, Wilson-Aggarwal, Stevens, & Spottiswoode, 2016) as well as the ability for incubating adults to detect and escape from approaching predators (Götmark, Blomqvist, Johansson, & Bergkvist, 1995). Understanding the role of vegetation will provide us with a fuller picture habitat selection in *H. ostralegus*, and may allow us to better predict future changes in territory settlement patterns.

Long-term flooding risk and environmental predictability

Increasing mean nest elevation in *H. ostralgeus* will reduce the detrimental impacts of extreme flooding events in our study population (van de Pol et al., 2010). However, the strength of observed nest elevation change is currently insufficient to keep pace with increases in maximum high tides (~0.52 cm/year nest elevation change vs. 0.8 cm/year change in maximum high tide; Bailey et al. 2017). Therefore, although our results provide encouraging evidence that habitat selection can

minimise the impacts of ECEs, it seems that, at least in this case, such responses are insufficient to fully alleviate the consequences of increased ECE frequency.

The future effectiveness of conspecific density and fledgling output as habitat selection cues is also dependent on the level of environmental predictability (temporal autocorrelation), which is itself affected by the frequency of ECEs (Canale & Henry, 2010). When ECEs are infrequent, environmental predictability is high and habitat selection cues that use information from previous time periods, such as conspecific density and fledgling output, will be reliable predictors of future conditions. As ECEs become more frequent, environmental predictability will diminish, which reduces the effectiveness of habitat selection strategies that rely on cues from previous time periods (Brandl, Griffith, & Schuett, 2018; Erwin, Nichols, Eyler, Stotts, & Truitt, 1998). In conditions of low environmental predictability, opportunistic habitat selection strategies that require limited prior information may instead be favoured by natural selection (Boulinier & Danchin, 1997; Doligez, Cadet, Danchin, & Boulinier, 2003; Bocedi, Heinonen, & Travis, 2012; Schmidt, Johansson, & Betts, 2015). Such strategies can involve increased juvenile dispersal (Friedenberg, 2003; Oro, Tavecchia, & Genovart, 2011) and low site fidelity of breeding birds (Erwin et al., 1998) leading to what has been termed 'nomadic breeding' (Crawford, Dyer, & Brooke, 1994). However, if the frequency of ECEs continues to increase to the point where such events are particularly common, environmental predictability will again be high and conspecific density and fledgling output could be used as reliable cues. In this scenario, settlements would stop at lower elevations, as these will be consistently poor breeding areas, and only those locations reliably unaffected by flooding events would be used. In sites where all areas are prone to flooding this may even lead to abandonment of the breeding site. Future flooding frequency will depend greatly on rates of sea level rise and changes in wind and storm patterns (van de Pol et al., 2010), and so it is unclear whether current habitat selection strategies used by *H. ostralegus* will continue to be effective in the future or whether other strategies, like nomadic breeding, will be favoured. More generally, considering changes in

environmental predictability will be necessary to predict how any organisms will respond to changes in ECE frequency.

Generalisation to other species

We present an example of organisms using habitat selection to minimise the detrimental effects of increasingly frequent ECEs. This has particular relevance for other coastal species that are likely to experience similar patterns of increased flooding (Bayard & Elphick, 2011; Pike & Stiner, 2007; Valdes, Hunter, & Nibbelink, 2016; van de Pol et al., 2010) ; however, these results may also have broader relevance for other organisms, although this may depend on the nature of the study system and the type of ECEs experienced. Coastal flooding has severe but localised impacts, leaving other locations within close proximity largely unaffected. Such a scenario should be easier for organisms to respond to as only small changes in habitat use can provide substantial benefits. In comparison, other ECEs, such as droughts or heatwaves, are far less localised and so will affect a much broader (even continental) geographic area (Schär et al., 2004). This will likely mean that much larger, and more costly, responses will be required by individuals to minimise ECE impacts. When effects of ECEs cover larger geographic areas the ability for organisms to respond through habitat selection will be affected by the costs of dispersal (Bonte et al., 2012), mobility, levels of habitat connectivity, and degree of habitat specialisation (Cornelius, Awade, Cândia-Gallardo, Sieving, & Metzger, 2017; Cote et al., 2017; A. E. Martin & Fahrig, 2018). Birds may be particularly well suited to deal with ECEs as they are highly mobile, while less mobile taxonomic groups, such as arthropods, may have less capacity to respond. Species that are less capable of using habitat selection to avoid future ECEs may instead need to rely on fine-scale micro-habitat to minimise the acute effects of these events (R. O. Martin et al., 2015). Therefore, while our results are encouraging, similar studies that encompass different types of ECEs and less mobile taxonomic groups should be conducted to understand whether our findings are broadly generalisable outside coastal nesting birds.

Conclusions

Anthropogenic climate change poses a serious threat to the viability of natural systems, particularly due to the increased frequency of extreme climatic events (ECEs). In this paper, we show that a population of ground nesting shorebirds has been able to minimise the effects of more frequent flooding events through habitat selection. Although these results are encouraging, we expect that both the rate of the change and the mechanism behind the change will be insufficient to cope with predicted increases in flooding frequency. This is one of the first such studies to consider this topic and more research is needed to understand whether such conclusions are broadly generalisable to other species.

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Data Accessibility:

Code and data are available on GitHub (https://github.com/LiamDBailey/Baileyetal_2019_JAE) and archived on Zenodo http://doi.org/10.5281/zenodo.3018357 (Bailey 2019).

Author contributions:

LDB and MvdP conceived the ideas; all authors contributed to data collection; LDB wrote the manuscript and analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

Figure captions:

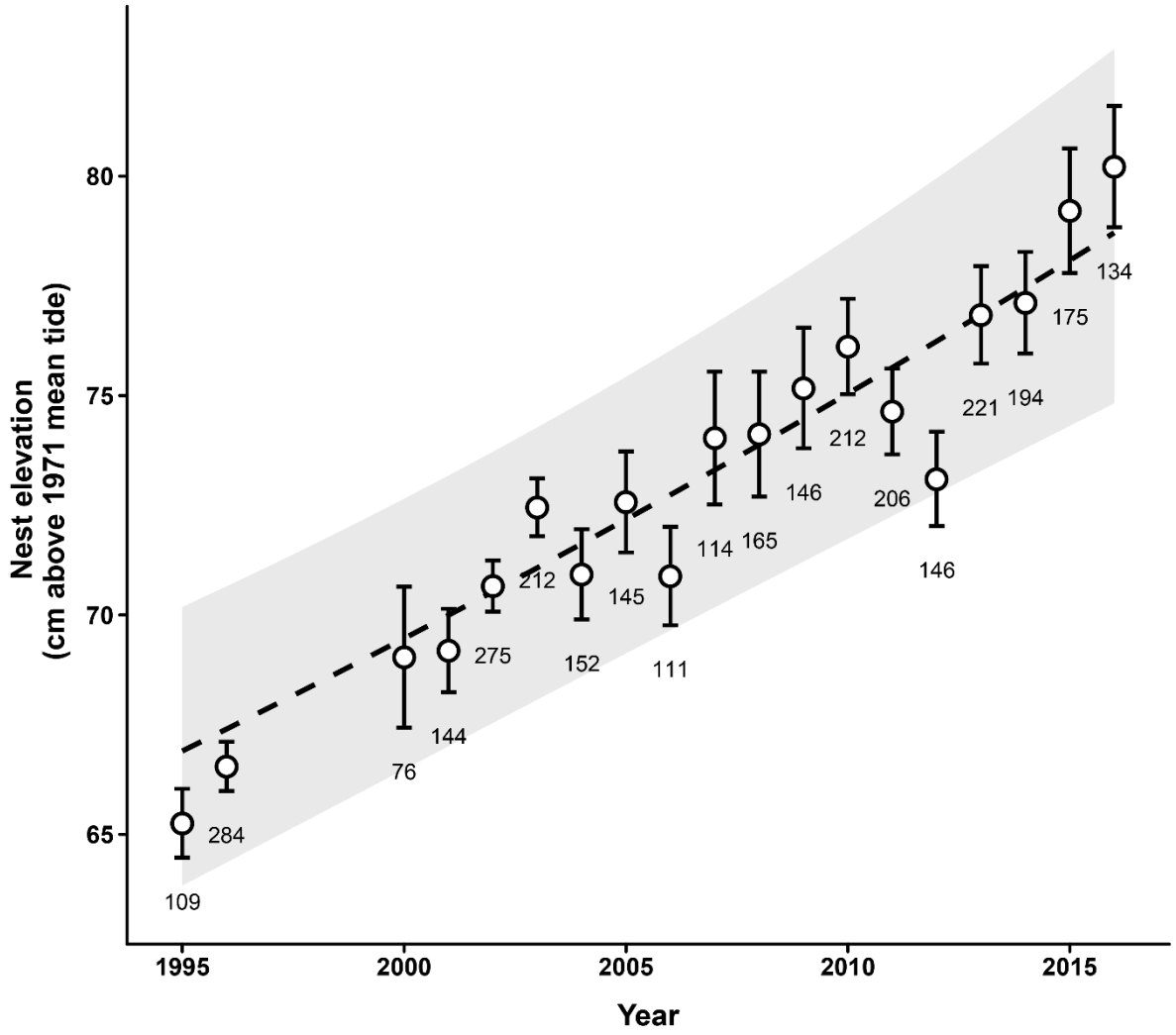

Figure 1: Change in mean nest elevation of *Haematopus ostralegus* over time. Nest elevation increased between 1995 and 2016. Points show annual mean nest elevation (± SE). These values are conditional estimates that show change in elevation within a single study sub-area (taken from the fitted model where study sub-area is fixed but all other parameters are allowed to vary). Raw data without sub-area correction are plotted in Fig. S5. Dashed line and grey band show model estimates and 95% prediction interval. Sample sizes are provided below each point.

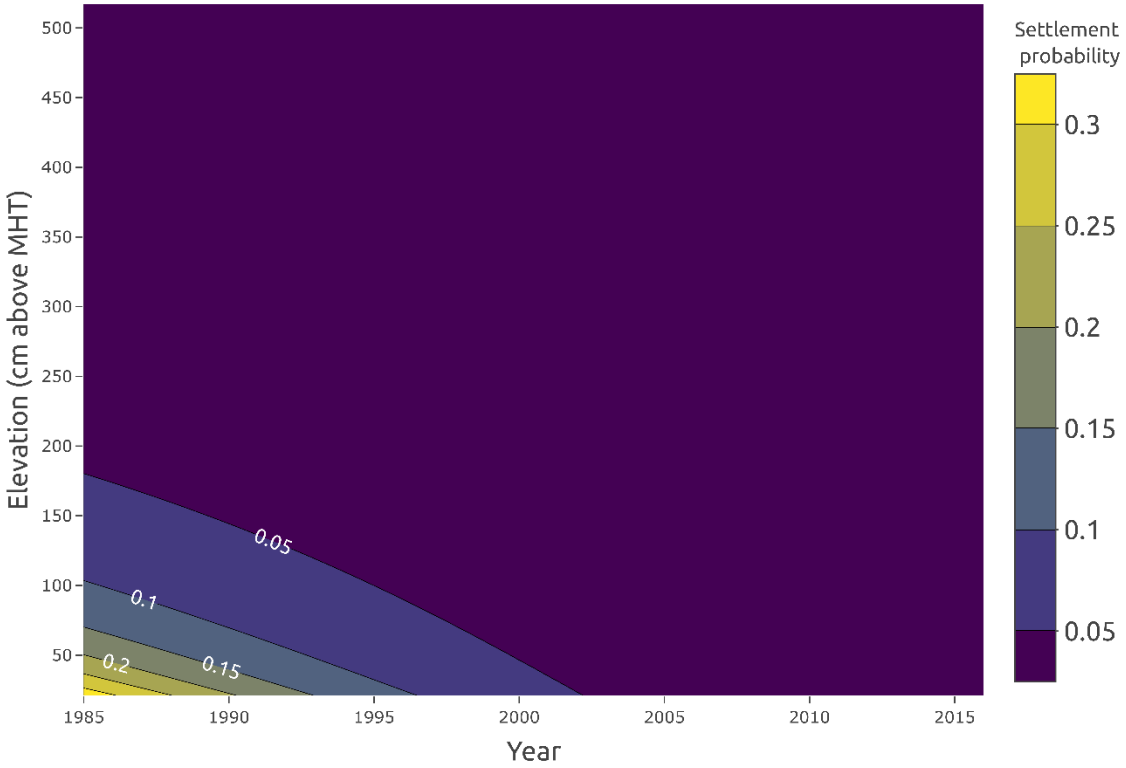

Figure 2: Relationship between elevation and probability of *Haematopus ostralegus* territory settlements over time (1985 – 2016). Yellow represents high settlement probability while low settlement probability is dark blue. In early years, birds are more likely to settle at low elevations. In more recent years there is no clear difference in settlement probability with elevation.

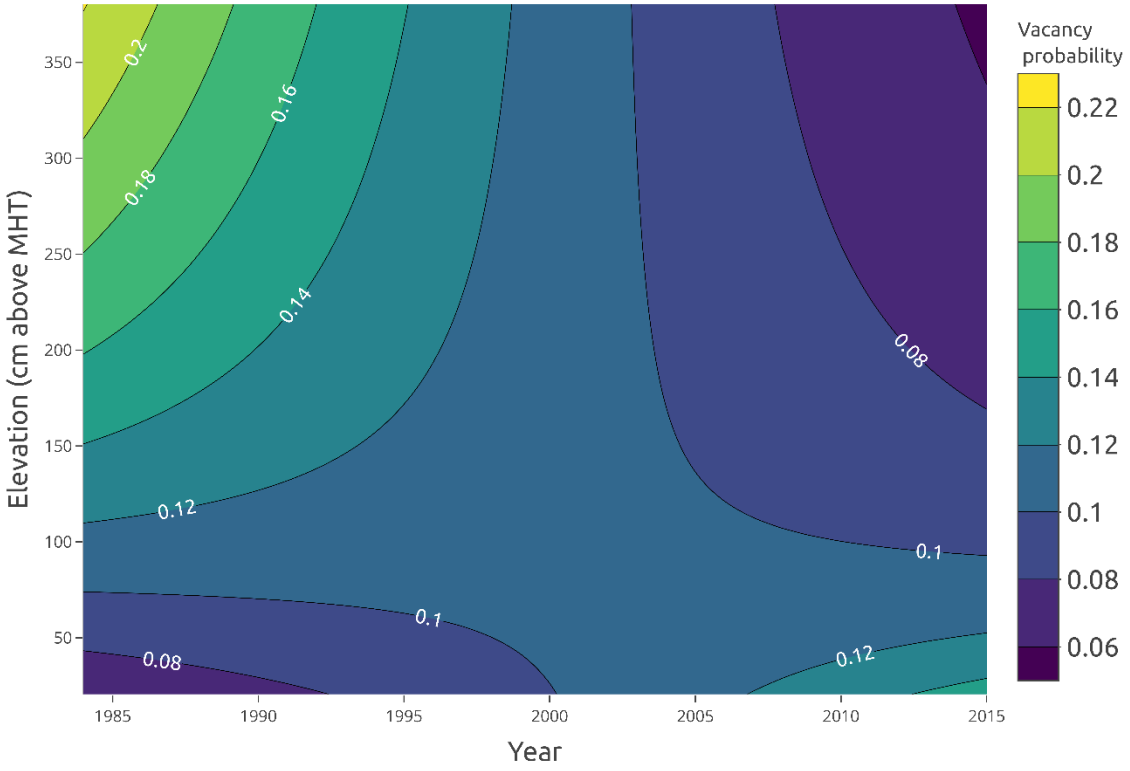

Figure 3: Relationship between elevation and the probability of territory vacancy in *Haematopus ostralegus* over time (1984 – 2015). Yellow regions represent high likelihood of territory vacancy, while low vacancy is in dark blue. In early years, higher elevation territories are more likely to be vacated. In later years low elevation territories are more likely to be vacated. However, the interaction effect was not supported using either 99.5% or 95% confidence intervals (Table S3).

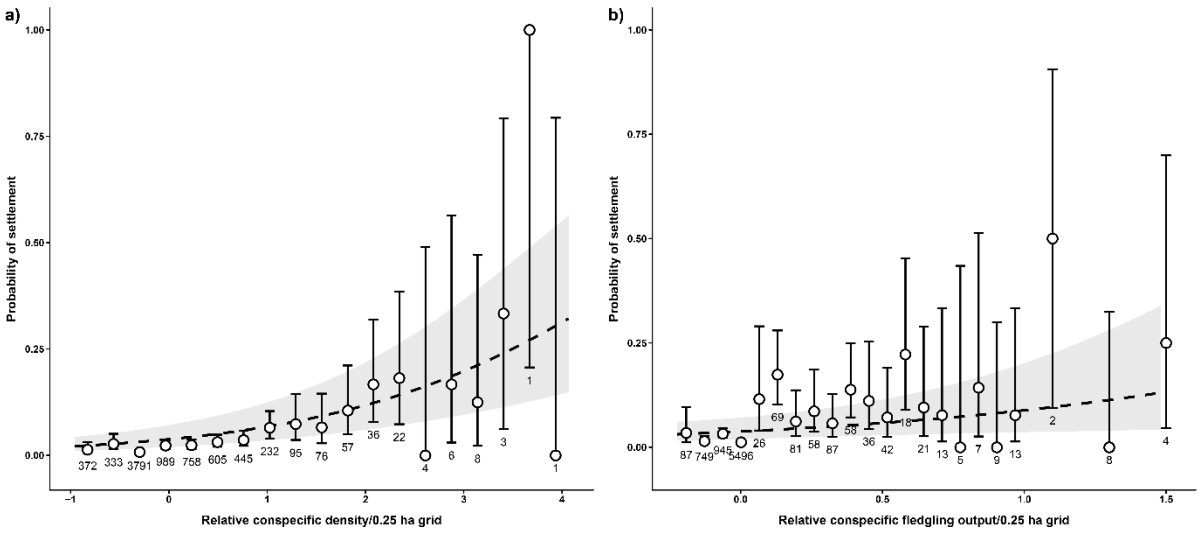

Figure 4: Relationship between a) relative conspecific density and b) relative conspecific fledgling output on the probability of territory settlement in *Haematopus ostralegus*. *H. ostralegus* were more likely to settle in areas with high conspecific density and higher fledgling output, suggesting these variables are used as cues for settlement. Dashed lines represent model estimates with 95% prediction interval, showing the effect of conspecific density and conspecific fledgling output on the probability of settlement with all other model parameters fixed at mean values. Sample size is provided below each point.

Tables:

Table 1: Model selection table comparing different habitat selection cues in *H. ostralegus*. Top models (ΔCAIC < 2) are shown here, for full model selection table see Table S4. Model comparison is conducted with conditional AIC (Vaida & Blanchard, 2005) and marginal and conditional R^2 values for each model are included following methods of (Nakagawa & Schielzeth, 2013). *w* denotes model weights (Burnham, Anderson, & Huyvaert, 2010). Parameter estimates of the top model using both 0.25 ha and 1 ha grid squares are shown in Table S5.

Elevation	Density	Food	Fledglings	CAIC	ΔAIC	*w*	R^2m	R^2c
+	+	-	+	1442.18	0.00	0.43	0.13	0.17
-	+	-	+	1443.92	1.74	0.18	0.14	0.18
+	+	+	+	1444.14	1.96	0.16	0.17	0.20

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